THE DEVELOPMENT OF THE EPIDERMIS AND HAIR CANALS IN THE MERINO SHEEP FOETUS

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Summary

A study has been made of the development of the epidermis and hair canals in Merino sheep foetuses ranging in age from 69 days to birth. The epidermis from several Merino lambs and adults has also been examined.

The keratinization of the epidermis, which takes place after the emergence of the first wool fibres, has been described in relation to the development of the wool follicles.

The development of hair canals in primary and secondary wool follicles in Merino sheep has been described for the first time. This is found to be a function both of the sebaceous gland cells which degenerate in the neck of the follicle, and of epidermal cells which keratinize at a separate locus.

I. Introduction

Although recent workers have devoted much attention to the development of wool follicles in sheep few studies have been made of the epidermis. Similarly, the formation of hair canals in sheep has not been adequately described.

In the present study the differentiation of the epidermis and hair canals is related to the "*F*" stages of wool follicle development as described by Hardy and Lyne (1956*b*, 1956*c*). Particular attention is given to the epidermis on the fleece-bearing area and no observations on the condition of the epidermis prior to the first appearance of wool follicles are recorded here. The "*F*" stages of follicle development were described under the following headings: *F*1, follicle plug; *F*2, pre-papilla; *F*3, papilla; *F*4, hair cone; *F*5, advanced hair cone; *F*6, hair formation; *F*7, hair in epidermis; *F*8, hair emerged. For primary (*P*) follicles, stage *F*2 was divided into stage *F*2*a*, when the rudiment of the sudoriferous gland appears, and stage *F*2*b*, when a sebaceous gland with differentiated cells is first recognized. In both *P* and secondary (*S*) follicles stage *F*3 was divided into *F*3*a*, when the dermal papilla at the base of the follicle has a depth less than its diameter, and *F*3*b*, when the depth of the papilla is equal to or (rarely) greater than its diameter.

II. Material and Methods

Twenty-four sheep foetuses (ranging in age from 69 to 145 days) described in a recent paper by Hardy and Lyne (1956*c*) provided some of the material for the present study. The other material examined came from eight medium-woolled Merino foetuses of known age (from 75 to 138 days). The epidermis of several Merino lambs and adults was also examined. The sampling positions, all from the fleece-bearing area of the trunk, included a midside sample for every foetus. Additional samples from the coronet region of two foetuses were used in the study of hair canal development.

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The histological methods were similar to those described by Hardy and Lyne (1956*c*). Fixation was with formalin or Zenker's fluid and sections were cut at 7 or 8 μ, occasionally thicker, and were stained with either haemalum and eosin or haemalum, eosin, and picric acid.

The terminology for wool follicles is that described by Hardy and Lyne (1956*a*). The terminology for epidermal strata is that defined in Hanson's (1947) detailed study of epidermal histogenesis in the rat and mouse, and is similar to that used by Pinkus (1910) for human material.

III. Development of the Epidermis

From stage *F*1 to stage *F*7 of the central primary (*PC*) wool follicles, the epidermis on the lateral regions of the trunk consists of three layers: the stratum germinativum, the stratum spinosum, and the periderm (Figs. 1(*a*) and 1(*b*)). When the *PC* follicles reach stage *F*8 the periderm is replaced by the stratum corneum (Figs. 1(*c*) and 1(*d*)). In all the post-natal material examined the epidermis remains thin and retains the same simple structure that it had at birth (Fig. 1(*e*)).

(*a*) *Stratum Germinativum*

The stratum germinativum, or basal layer of the epidermis, consists of undifferentiated cells which give rise to the other epidermal strata as well as the first wool follicles (Fig. 1(*a*)). Its cells usually form a conspicuous single layer adjacent to the basement membrane, and the nuclei, at first cuboidal in shape, are very large in proportion to the volume of the cells. The outlines of the cells themselves are irregular and indistinct.

When the first *S* fibres emerge the stratum germinativum is still a continuous layer but it may be an incomplete layer at birth (Fig. 1(*e*)).

(*b*) *Stratum Spinosum*

The stratum spinosum, superficial to the stratum germinativum, is well established when only the *PC* follicles are present and it can be easily recognized as a continuous layer when the first fibres emerge (Fig. 1(*c*)). It consists of differentiating cells with relatively more cytoplasm and more clearly defined cell outlines than the cells of the stratum germinativum. Three or four cell layers can be recognized and the cells become flatter as they approach the skin surface. Within the stratum spinosum the first indication of the formation of some of the hair canals (described in Section IV) is seen when the *PC* follicles reach stage *F*2*b*.

When the first *S* fibres emerge, the stratum spinosum still consists of several layers but it is no more than an incomplete single layer of cells at birth (Fig. 1(*e*)).

(*c*) *Periderm and Stratum Corneum*

The periderm is the outermost layer of the epidermis and, on the lateral regions of the trunk, it persists at least until the first *PC* follicles reach stage *F*8 (Fig. 1(*c*)). The cells usually have dense eosinophilic cytoplasm. In sections cut at right angles to the skin surface the periderm cells appear to be flattened and have deeply staining

flattened nuclei; when viewed from the surface they appear as large polygonal cells with distinct cell outlines and pale round nuclei. Throughout this period the periderm appears to be a continuous layer one or two cells thick.

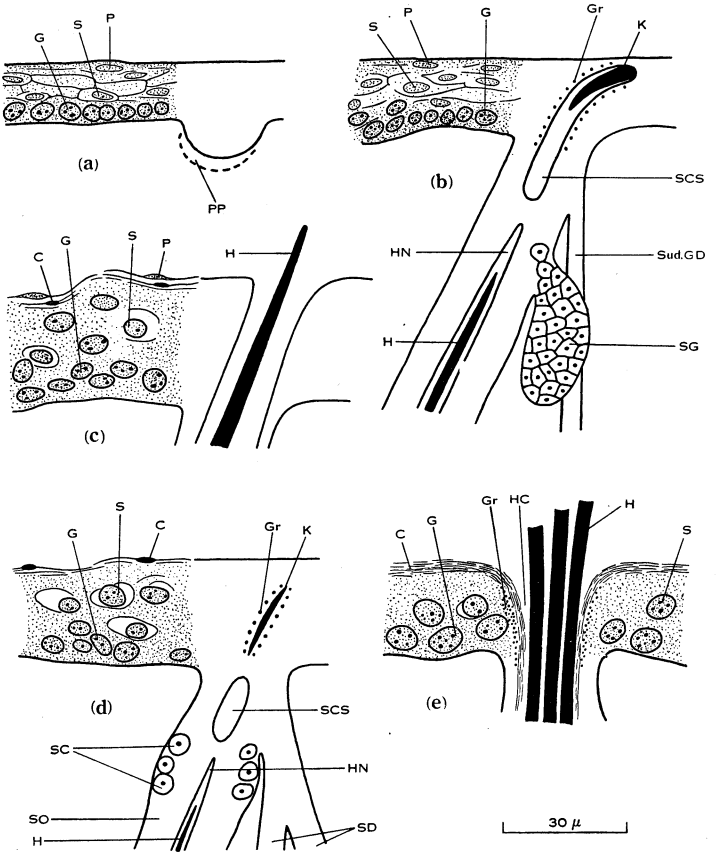

Fig. 1.—Camera lucida drawings of the epidermis of Merino foetuses during the period of wool follicle development. *C*, stratum corneum; *G*, stratum germinativum; *Gr*, cells containing keratohyalin granules; *H*, wool fibre; *HC*, hair canal; *HN*, hair cone; *K*, keratinized cells of hair canal; *P*, periderm; *PP*, pre-papilla; *S*, stratum spinosum; *SC*, sebaceous cells; *SCS*, space formed by disintegration of sebaceous cells; *SD*, derived secondary follicles; *SG*, sebaceous gland; *SO*, original secondary follicle; *SudGD*, sudoriferous gland duct. (*a*) Lateral lumbar region of 69-day foetus. The most advanced follicles are at state *F*1. (*b*) Mid-lateral region of trunk of 98-day foetus. Most advanced follicles at stage *F*6. (*c*) Posterior cervical region of 101-day foetus. Most advanced *PC* follicles at stage *F*8. (*d*) Sternal region of 108-day foetus. Most advanced *SO* follicles at stage *F*6. (*e*) Mid-lateral region of trunk 4 days after birth.

When the first *PC* fibres emerge, cells containing small flattened pyknotic nuclei are seen immediately below the periderm (Fig. 1(*c*)). These nucleated cells constitute the beginning of the stratum corneum which is at first parakeratotic (i.e. it shows imperfect cornification). For a time the periderm cells remain above the stratum corneum but none can be distinguished after the first *S* follicles reach stage *F*6 (Fig. 1(*d*)). The cells of the periderm become greatly flattened but they do not pass through

the same stages of keratinization as are seen in the formation of the definitive stratum corneum.

After the emergence of the *S* fibres, the stratum corneum has its typical structure with several layers of cornified cells, and the pyknotic nuclei have disappeared (Fig. 1(*e*)).

(*d*) *Stratum Granulosum*

The stratum granulosum is absent or very poorly developed, except around the follicles and in the neck regions of the follicles (Fig. 1(*e*)).

IV. Development of the Hair Canals

The hair canals in the Merino foetus are formed by two separate processes—keratinization of cells in the epidermis and disintegration of sebaceous cells which have migrated to the neck of the follicle. The initial stages of differentiation of the epidermal cells are independent of those of sebaceous cells and the two processes are described separately. In the epidermal cells there is keratohyalin granulation and keratinization which is followed by the appearance of an intercellular space, while in the sebaceous cells there is cell degeneration followed by space formation. Eventually a continuous canal runs from the follicle neck to the upper part of the epidermis.

(*a*) *Stages of Hair Canal Development*

Epidermal Stages

Stage A: *Granulation.*—This stage begins with the appearance of keratohyalin granules within one or more cells of the stratum spinosum, immediately above the ental (obtuse angle) side of the follicle, or within the upper neck region of the follicle.

Stage B: *Keratinization.*—The granulation extends to the surrounding cells and those in the centre become keratinized (as judged by the appearance of thin sheets of keratin).

Stage C: *Space Formation.*—In fixed material a tube-shaped space forms within the region of keratinizing cells.

Sebaceous Cell Stages

Stage A: *Migration.*—Differentiated cells from the sebaceous gland move into the neck region of the follicle as isolated cells or as a column of cells connected with the gland.

Stage B: *Degeneration.*—The sebaceous cells degenerate (i.e. the nuclei and cell outlines disappear) within the neck region of the follicle.

Stage C: *Space Formation.*—As the sebaceous cells degenerate one or more spaces filled with fat and detritus are formed within the follicle neck.

Completed Hair Canal

The hair canal extends from above the sebaceous gland to the level of the stratum corneum.

Some or all of the above stages may be recognized in the development of both *P* and *S* follicles (Fig. 2; Plates 1 and 2).

(*b*) *Primary Follicles*

The epidermal stages in the formation of the hair canal of a *P* follicle usually occur within the stratum spinosum of the epidermis. Epidermal stage A (Fig. 2(*a*); Plate 1, Fig. 1) usually precedes sebaceous cell stage A but these two stages may begin at about the same time (Fig. 2(*b*); Plate 1, Fig. 2), when the follicle is at stage *F3a* or *F3b*. In skin from the coronet, epidermal stage A has been observed as early as follicle stage *F2b*. Further development of the epidermal portion of the hair canal proceeds upwards and downwards approximately in the direction of the long axis of the follicle until it reaches the periderm above and the level of the stratum germ-

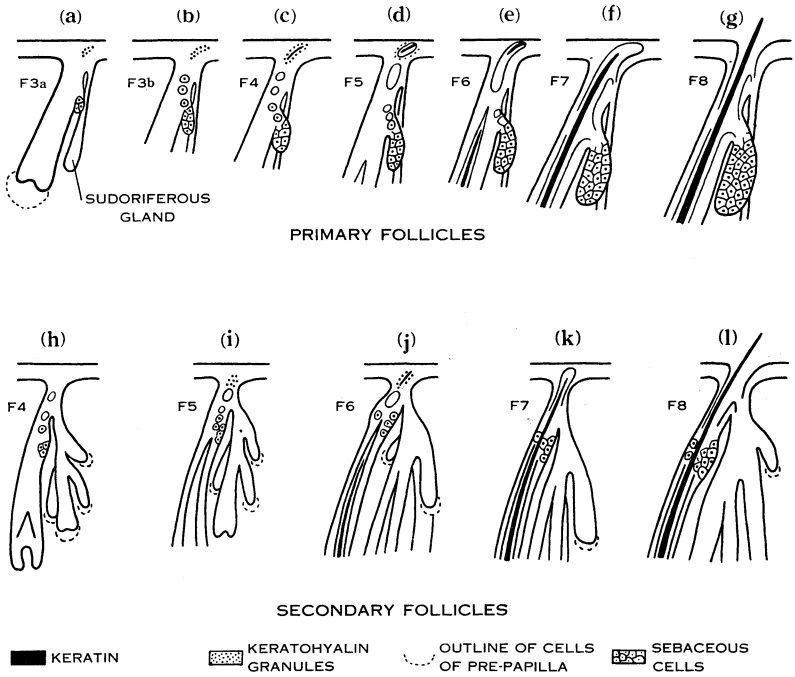

Fig. 2.—Stages in the development of hair canals in the Merino foetus. (*a*)–(*g*), primary follicles; (*h*)–(*l*), secondary follicles.

inativum below. Epidermal stage B usually appears at the same time as sebaceous cell stage B (Fig. 2(*c*); Plate 1, Fig. 4) but, in skin from the coronet, it may begin at sebaceous cell stage A (Plate 2, Fig. 1). Sebaceous cell stage C usually precedes epidermal stage C (Fig. 2(*d*); Plate 1, Fig. 3; Plate 2, Fig. 2).

The hair canal may be completed (Fig. 2(*f*); Plate 1, Fig. 5) as early as stage *F3b* but this more frequently occurs at stage *F4* to *F5*. At stage *F7* the hair canal is always completed. The upper part of the completed hair canal is usually bent so that it is almost parallel with the skin surface.

No difference between the manner of hair canal formation in central and lateral primary follicles has yet been observed.

(c) *Secondary Follicles*

The formation of the hair canal of an original secondary (*SO*) follicle (Figs. 2(*h*)–2(*l*); Plate 1, Figs. 6–9) is similar in most respects to that described above for a *P* follicle, except that:

(i) Epidermal stage A (Fig. 2(*i*); Plate 1, Fig. 7) usually occurs later than sebaceous cell stage A (Fig. 2(*h*); Plate 1, Fig. 6) and neither has been observed before follicle stage *F*4.

(ii) Epidermal stage A frequently begins within the upper neck region of the follicle rather than in the epidermis proper.

(iii) The *SO* follicle provides the common hair canal for all of the derived secondary (*SD*) follicles (Figs. 2(*h*)–2(*l*); Plate 1, Figs. 6 and 8) which may arise from it.

(iv) The characteristic bending of the upper part of the hair canal of *P* follicles has not been observed with *S* follicles (Plate 1, Fig. 9).

V. Discussion

In the Merino sheep the first cornified layers of the epidermis were parakeratotic, and were not replaced by a normal stratum corneum until the first *S* fibres had emerged from the skin surface. As the *P* fibres had already begun to emerge before the parakeratotic layers were formed, there was no epitrichium in the sense used by Hanson (1947) of "the keratinized layers which are shed when the first hair coat emerges". Pinkus (1910) and Hanson (1947) considered that differentiation of the periderm probably takes place by parakeratosis in the human and in the rat and mouse.

The fully differentiated epidermis of the fleece-bearing area remained thin up to the time of birth and throughout post-natal life, and lacked a continuous stratum granulosum. This is in agreement with the observations of Spöttel and Tänzer (1923) who considered that the reason for the relatively slight development of the epidermis in sheep must be sought in the dense hairy covering.

The keratinization process in the hair canals was different to that in the epidermis. It began much earlier in foetal life, and the cornified cells differentiated from cells loaded with keratohyalin granules. After the emergence of the wool fibres the follicle necks continued to have a keratohyalin layer (stratum granulosum) beneath the cornified cells.

Diem (1907) briefly described hair canal development in the sheep and his observation that the formation of the hair canal is a function both of the sebaceous gland cells, which degenerate in the neck region of the follicle, and of epidermal cells, which keratinize some distance above them, has been confirmed. Diem considered that the sebaceous glands are only secondarily responsible for the formation of the epidermal portion of the hair canal, in that they possibly widen the canal by means of the secretion introduced into the lumen. Later authors appear to have overlooked the observations made by Diem. Duerden and Ritchie (1924) attributed hair canal formation to the distintegration of cells within the solid follicle neck, near the place of origin of the sebaceous gland; at the same time, similar changes

take place among the sebaceous cells so that a short duct is formed. The observations of Marks (1895), Spöttel and Tänzer (1923), and Wildman (1932) are incomplete in that they attributed the origin of the hair canals to the activity of the sebaceous cells alone.

The epidermal stages in the formation of hair canals in mouse pelage hair follicles (Hardy 1949) and mouse vibrissa follicles (Davidson and Hardy 1952) are similar to those described for wool follicles in sheep, except that the keratinization process for vibrissa follicles begins at the surface of the epidermis. No connection between sebaceous gland cells and hair canal formation in the mouse was observed by these authors.

VI. Acknowledgments

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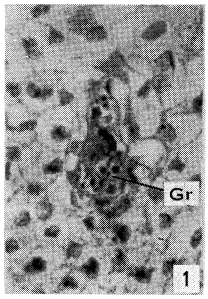
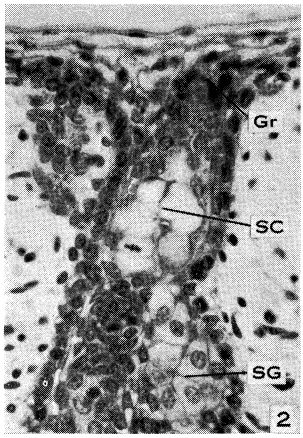
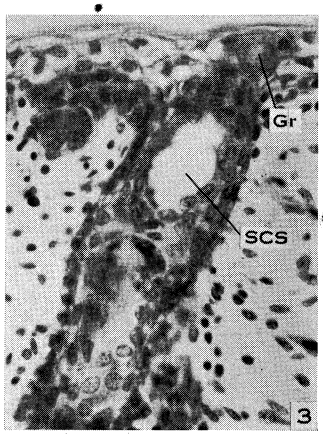
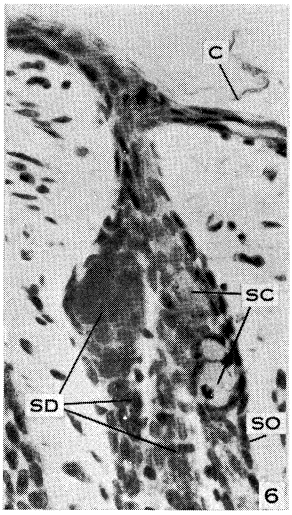
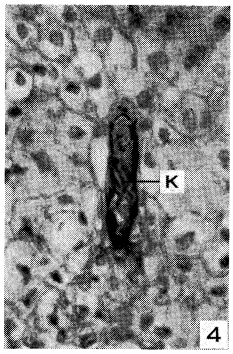
EPIDERMIS AND HAIR CANALS IN MERINO SHEEP

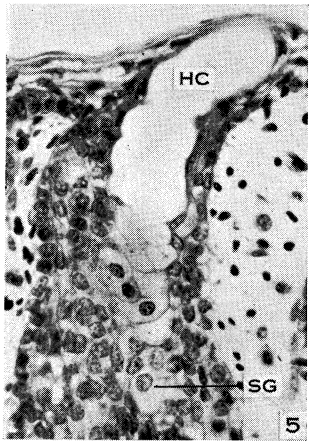












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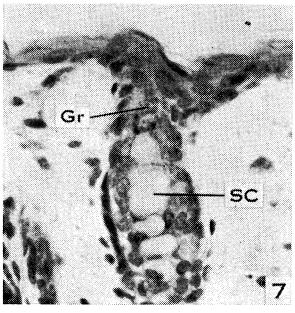
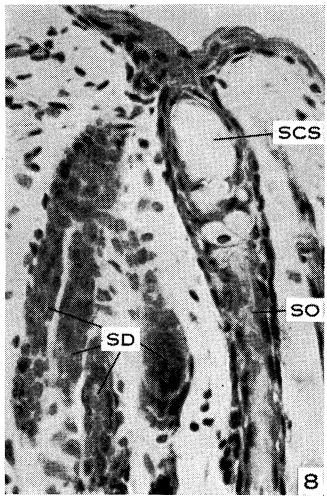
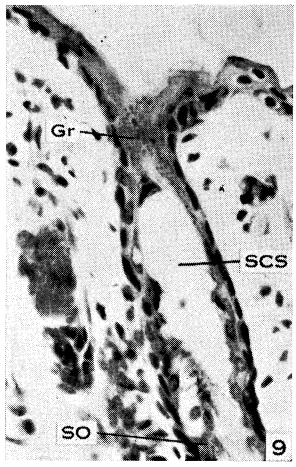
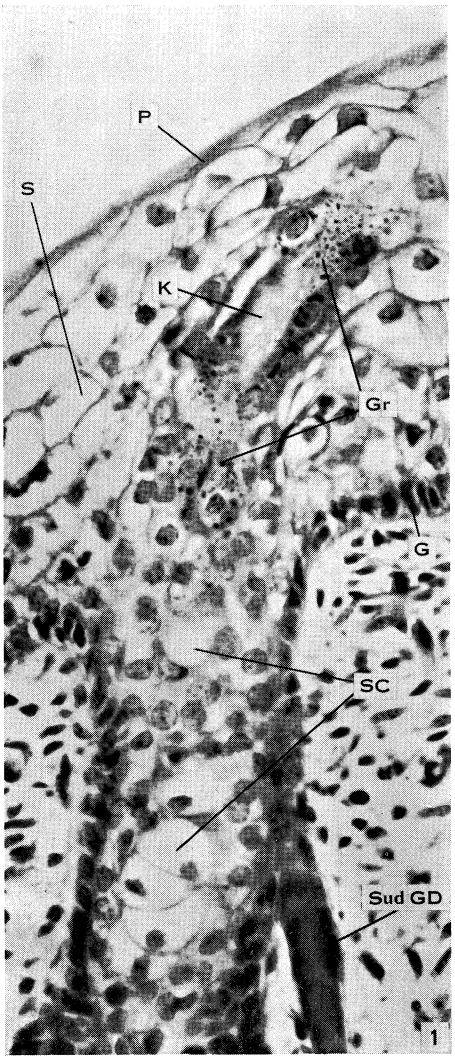
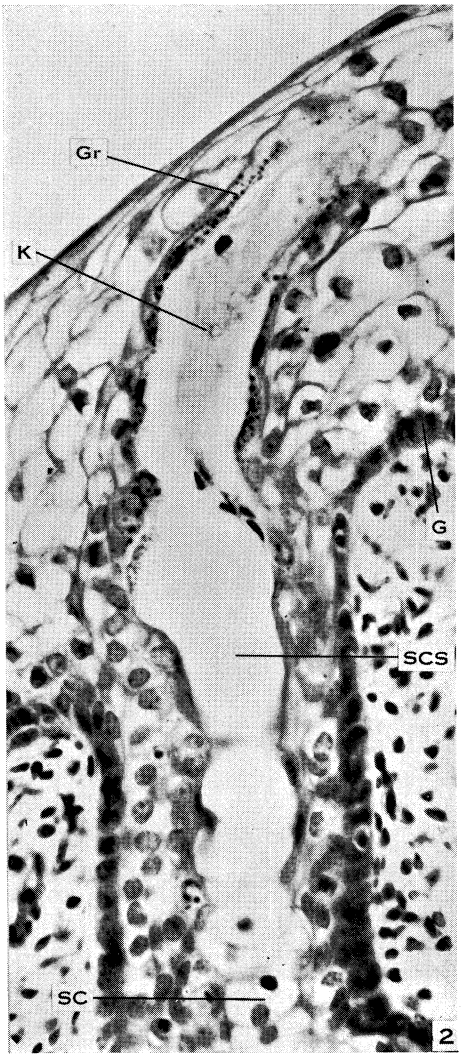






EPIDERMIS AND HAIR CANALS IN MERINO SHEEP





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Explanation of Plates 1 and 2

All figures are of sections through skin from Merino foetuses. The staining is with haemalum, eosin, and picric acid. Lettering as for Figure 1

Plate 1

Development of hair canals. Figs. 1–5.—Primary follicles: sections from mid-lateral region of the trunk. Figs. 6–9.—Secondary follicles: longitudinal sections of upper parts of *SO* follicles from shoulder region of 125-day foetus

Fig. 1.—Horizontal section of epidermis from 81-day foetus with hair canal of *P* follicle at epidermal stage A.

Fig. 2.—Vertical section of upper part of skin from 98-day foetus with hair canal of *P* follicle at epidermal stage A and sebaceous cell stage A.

Fig. 3.—Vertical section of upper part of skin from 98-day foetus with hair canal of *P* follicle at epidermal stage A and sebaceous cell stage C.

Fig. 4.—Horizontal section of epidermis from 91-day foetus with hair canal of *P* follicle at epidermal stage B.

Fig. 5.—Vertical section of upper part of skin from 98-day foetus with completed hair canal of *P* follicle.

Fig. 6.—Hair canal of *SO* follicle at sebaceous cell stage A.

Fig. 7.—Hair canal of *SO* follicle at epidermal stage A. and sebaceous cell stage B.

Fig. 8.—Hair canal of *SO* follicle at sebaceous cell stage C.

Fig. 9.—Hair canal of *SO* follicle at epidermal stage A and sebaceous cell stage C.

Plate 2

Development of hair canals. Vertical sections of upper part of skin from coronet region of 80-day foetus (believed to be Merino)

Fig. 1.—Hair canal of *P* follicle at epidermal stage B and sebaceous cell stage A. Note that the hair canal is formed by two separate processes—keratinization of cells in the epidermis and disintegration of sebaceous cells which migrate to the neck of the follicle.

Fig. 2.—Hair canal of *P* follicle at early epidermal stage C and sebaceous cell stage C. Note the keratohyalin layer beneath the cornified cells within the epidermal portion of the hair canal.